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Seasonal dynamics of plankton communities and water chemistry in a eutrophic wetland (Lake Monger, Western Australia): implications for biomanipulation

Mark A. Lund[A] and Jennifer A. Davis

School of Biological and Environmental Sciences, Murdoch University, WA 6150, Australia
[A]Present address: Centre for Ecosystem Management, Edith Cowan University, Joondalup WA 6027, Australia. email. M.Lund@cowan.edu.au

Abstract. In a large (70 ha) shallow (<2m deep) eutrophic wetland investigated between November 1988 and October 1989, there were marked seasonal changes in water quality and the composition of zooplankton, and to a lesser extent phytoplankton communities, with three distinct groupings evident: summer, winter–spring and autumn. Summer conditions were characterized by high levels of total P (689±198 μg L^{-1}), N limitation, blooms of *Microcystis aeruginosa* (mean chlorophyll *a* = 466±30 μg L^{-1}) and zooplankton communities dominated by cyclopoid copepods (*Mesocyclops* sp. and *Microcyclops* sp.). Winter–spring conditions were characterized by Secchi disk transparencies to the bed (chlorophyll *a* <50 μg L^{-1}), low total P (71±40 μg L^{-1}) and zooplankton communities dominated by *Daphnia carinata* King. Autumn conditions represented an intermediate state between these two. Significant linear relationships were recorded between chlorophyll *a* and total P and between chlorophyll *a* and *D. carinata*. Abundances of hemipteran predators (*Anisops* sp.) were correlated with *D. carinata*, but the relationship did not appear to be causal. The decline in *D. carinata* in summer was attributed to food limitation. Reductions in nutrient inputs to the lake in 1990–91, resulted in improved water quality and high abundances of *D. carinata* during summer.

Introduction

Over 10 000 wetlands and >80% of the human population of Western Australia coexist on the Swan Coastal Plain (SCP) between Moore River and Mandurah (Hill *et al.* 1996). Agriculture and urban development are responsible for the eutrophication of many of these wetlands. Eutrophication and cyanobacterial blooms have been identified as a serious problem in Australia (Aplin 1983; Hötzel and Croome 1994). However, relatively few studies have examined lentic plankton ecology or responses to eutrophication in any detail (e.g. Gordon *et al*. 1981; Merrick and Ganf 1988), although Mitchell and Williams (1982*a*, 1982*b*) studied zooplankton in sewage treatment ponds in South Australia. In Western Australia (WA), most studies have described water quality rather than ecological attributes (e.g. Congdon 1986; Davis and Rolls 1987; Bayley *et al*. 1989; Lund and Ryder 1998; Lund in press).

Vollenweider (1968) redefined lake management making it possible to quantitatively explain and predict bottom-up relationships within lakes. These relationships did not, however, fully account for all the variability observed in chlorophyll *a* concentrations among lakes; subsequently, Shapiro and Wright (1984) suggested that top-down control was responsible for some of the variability and that this form of control could be enhanced to manage lakes. Top-down control (biomanipulation), although successful in only ~20% of cases (Matveev *et al*. 1994), has nevertheless resulted in considerable research into the interrelationships between fish, zooplankton, phytoplankton and nutrients. There has been increasing interest in biomanipulation in Australia, although as a technique it remains largely untested (see Boon *et al*. 1994; Matveev *et al.* 1994). This paper describes seasonal changes and inter-relationships between zooplankton, phytoplankton, and nutrients within a shallow eutrophic wetland on the SCP. The strength and importance of top-down and bottom-up controls of algal biomass and the possible consequences for biomanipulation are discussed.

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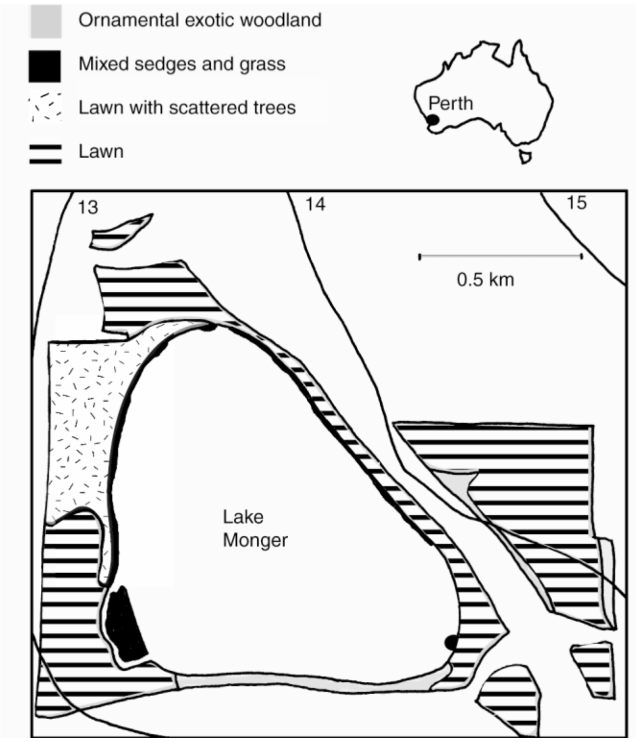

Fig. 1. Location of Lake Monger, showing vegetation types, Mounts Bay Drain (●) and the groundwater contours (height in m AHD).

Methods

Study site

Lake Monger (32°4′S,115°20′E) is a shallow (<2m deep) lake on the SCP near central Perth (Fig. 1). The SCP is a series of parallel dunal systems of varying ages between the Indian Ocean to the west and the Darling Scarp to the east. Lake Monger is a surface expression of the water table and is situated in the limestone-rich Spearwood Dune system. The lake (area 70 ha) and surrounding public park (110 ha) are visited by >12 000 people per week for passive recreation (Middle 1988). Dredging and infill with sanitary landfill has substantially altered the physical dimensions of the lake. The hydrology has been modified by stormwater inputs from 23 urban drains (catchment of 597.8 ha; Perth City Council, personal communication). Drains contributed ~589 ML of water to the lake in 1989 (based on a conservative runoff coefficient of 0.13 derived from Bayley *et al.* 1989), while groundwater contributed 161 ML (Main Roads Department, unpublished). The depth of the lake is artificially maintained during summer by the addition of groundwater. Excess water is allowed to flow to the Swan River in winter via the Mounts Bay Drain. Nutrient loads in the drains have not been measured; however, in nearby Lake Claremont, drains were the main contributors of P, carrying soluble reactive phosphorus (SRP) concentrations ranging between 16 and 500 µg L^{-1} (Lantzke *et al.* 1989). Davis *et al*. (1993) recorded total P (TP) levels of 0.9–1.4 mg g^{-1} (dry wt) in the sediment of Lake Monger in 1989, close to the maximum recorded in a study of >40 wetlands on the SCP. Qiu and McComb (1994) recorded TP levels of 1.3 mg g^{-1} in the sediment in 1993. Groundwater enters the lake on the south-western side, intersecting landfill (sand and domestic waste) across 1.1 km of shoreline. Nutrient concentrations of 120–7200 µg L^{-1} of nitrate and 50–1070 µg L^{-1} of SRP were recorded in upstream groundwater in 1985, with higher values at the south-eastern end where the landfill was youngest (Main Roads Department, unpublished). Adding to the nutrient load of the groundwater are fertilizers used on the lawns in the public park. The lawns surrounding Lake Monger received 70 kg P and 300 kg N in September–October 1988, 455 kg N in December–January 1988–89, and 40 kg P and 240 kg N in both March–April and September–October 1989 in several fertilizer formulations (Perth City Council, personal communication).

Sampling methods

Five randomly located sites (>10 m from the edge of the lake) were sampled every 2–4 weeks, on 17 occasions, between November 1988 and October 1989. Water depth, Secchi depth (0.2 m disk) and dissolved oxygen–temperature profiles (YSI Model 58) were measured at each site. Surface (0.2 m) and bottom water samples were collected with a Van Dorn bottle. A sub-sample of each sample was chilled (4°C) for later determination of pH (Hanna HI 8424), alkalinity and conductivity (Hanna HI 8733). Alkalinity was stoichiometrically divided into HCO_3^{-2}, CO_3^{-2} and OH^{-1} and used to calculate free CO_2 (Anon. 1989). Further sub-samples were frozen for determination of total Kjeldahl N (TKN) and TP and filtered (Whatman GF/C) and frozen for subsequent analysis of ammonia and SRP. The filter paper was frozen for subsequent determination of chlorophyll *a* using the dimethylformamide extraction method of Moran and Porath (1980) and Moran (1982). Nutrients were analysed according to the methods of APHA (Anon. 1989), with the exception that a perchloric acid digestion was used for TKN which resulted in poor recoveries — a correction factor has been applied to the results to account for this (see Lund 1992). Maximum–minimum thermometers (surface and bed) attached to a buoy in the centre of the lake were read and reset on each sampling occasion.

At each site an oblique plankton tow (net 0.34 m diameter, 53 µm mesh) was pulled over a fixed distance to sample 0.5 m^3 of water at each site. Preliminary trials indicated that this approach produced quantitative results, and the short tow reduced the effects of clogging. Samples were preserved with 100% ethanol and subsequently divided into two fractions comprising a >250 µm sample in which zooplankton were identified and enumerated and a <250 µm sample in which the presence of phytoplankton genera was recorded. The presence of eggs in *Mesocyclops* sp. and *Daphnia carinata* King was recorded for ~100 randomly selected individuals on each sampling occasion. Australian Height Datum (AHD) records were obtained from the Water Authority of WA (now Water Corporation of WA) and meteorological data were obtained from Bureau of Meteorology (Perth).

The zooplankton and water quality data were $\log_{10}(x+1)$ transformed prior to analysis. Product Moment Correlation matrices were calculated between water quality parameters and zooplankton abundances. Simple linear regression was used to examine relationships between trophic levels following the approach of McQueen *et al.* (1986). Factor analysis (varimax rotation) was used to identify any multicolinearity that occurred in the correlation matrix. One-way analysis of variance (ANOVA) followed by Scheffe's pairwise comparisons was used to test for differences between seasonal groupings in water quality and zooplankton data sets. The zooplankton data were standardized by range to normalize the Kulczynski (Faith *et al*. 1987) association scores. The Gower metric (Williams *et al*. 1987) and Czekanowski (Belbin 1990) association measures were applied to the water quality and phytoplankton data respectively. The resulting association matrices were then classified (Unweighted Pair Group arithMetic Averaging (UPGMA)) and ordinated (Semi-Strong Hybrid multidimensional scaling (SSH)) using the PATN software package (Belbin 1989). A 3-dimensional solution was obtained from 100 random starts for each data set. Ordinations were compared by generalized Procrustean rotation (PROC) (Marchant 1990). Principal axis correlation (PCC) was used to examine linear correlation with the ordination spaces, the significance being tested by Monte Carlo techniques (Faith 1990).

Results

There were marked seasonal changes in water quality and zooplankton communities. Ordination and classification of the water quality data revealed three major groupings: summer (29 November 1988 to 7 February 1989; winter–spring (8 November 1988, 23 May 1989 to 24 October 1989); and autumn (7 March 1989 to 2 May 1989) (Fig. 2*a*). Similar groupings were also seen in the zooplankton (Fig. 2*b*) and phytoplankton (Fig. 2*c*) but with a higher degree of overlap between groups. Winter–spring was characterized by Secchi depths that extended to the lake bed, low chlorophyll *a*, low P levels, high ammonia concentrations and zooplankton dominated by *D. carinata* (Table 1). In autumn and summer, the lake had shallow Secchi depths, high concentrations of TP and chlorophyll *a* (blooms of *Microcystis aeruginosa*), and *Mesocyclops* sp. as the dominant zooplankton. The three ordinations were very similar to each other as indicated by the low root-mean-squared symmetric (RMS) error calculated between ordinations (water quality *v.* zooplankton 0.084; water quality *v.* algae 0.097; zooplankton *v.* algae 0.0974). An examination of the individual measures of fit between samples indicated that the greatest variation occurred between samples in summer and autumn in all three ordinations.

Water quality

Only surface water samples (the most complete data set) are considered here as no significant difference was found between surface and bottom water samples for most parameters (Fig. 3). The lake was not stratified, except briefly on one occasion in summer when a mean difference of 1.4°C was recorded between the top and bottom of the water column. Instantaneous water temperatures (recorded at the surface or bed) were generally poorly correlated ($r < 0.7$) with most meteorological and physico-chemical parameters, but maximum and minimum water temperatures (especially minimum) were highly correlated ($r > 0.7$; $P < 0.05$). Factor analysis revealed a high degree of multicolinearity between all parameters, with almost half of them associated with the first factor.

Conductivity was inversely related to water depth ($r = -0.81$; $P < 0.05$) reflecting the decrease in precipitation that resulted in evapo-concentration over summer and autumn. The effect was minor and unlikely to have had any significant effect on the biota, because the lake remained fresh (*sensu* Bayly and Williams 1981) throughout the year with conductivity ranging from 690 to 1142 µS cm^{-1}. Depth ranged from 0.9 to 1.4 m, and lake-bed topography was extremely uniform with depth varying <0.3 m between sites on any occasion.

Phosphorus concentrations increased markedly from winter to summer (mean ± s.e.; 71 ± 40 to 689 ± 198 µg TP L^{-1} and 16 ± 2 to 345 ± 13 µg SRP L^{-1} respectively). Similar seasonal changes in TKN were not recorded (3325–6384 µg L^{-1})

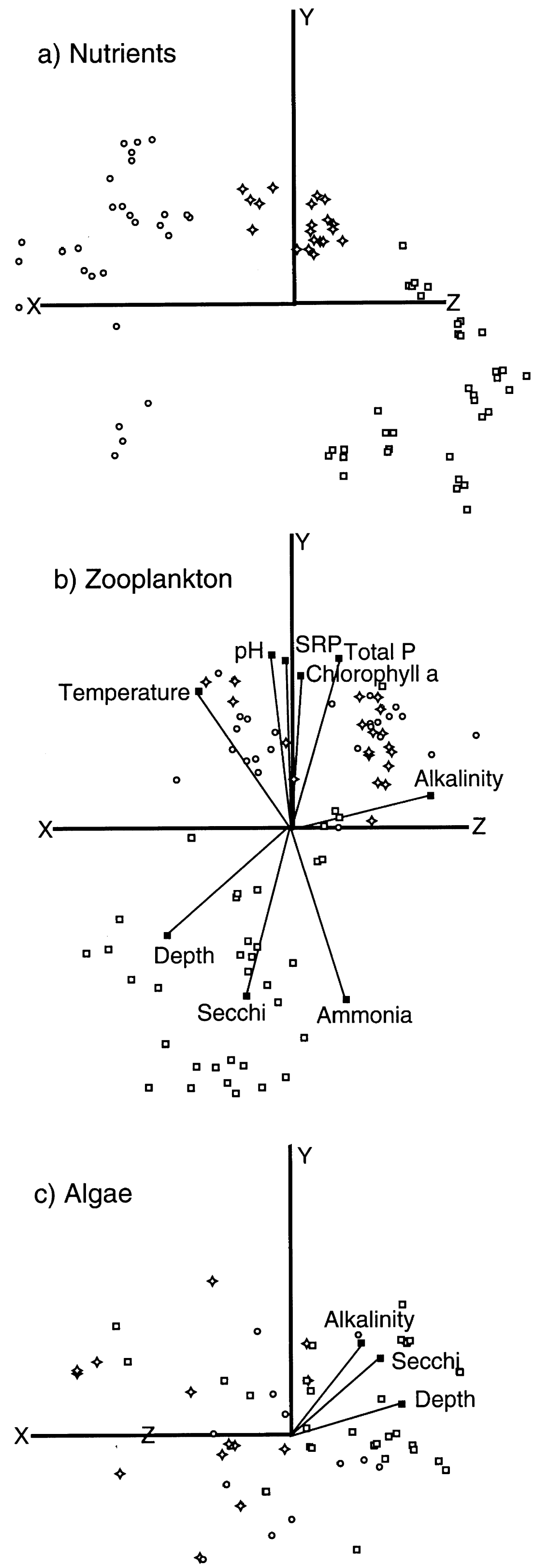

Fig. 2. Ordination plots showing three dimensions (axes all of equal length and centred on origin; arrows of equal length and show direction of PCC correlations within the ordination space). □ Winter–spring; ○ summer; ✧ autumn.

Table 1. Water quality and abundance of selected zooplankton taxa for each seasonal grouping

Values are mean ± s.e. Letters indicate no significant difference (P <0.05) between groupings; ANOVA and $\log_{10}(x+1)$-transformed data

	Summer	Autumn	Winter–Spring
Depth (m)	1.07 ± 0.03	0.86 ± 0.02	1.2 ± 0.02
Conductivity (μS cm^{-1})	845 ± 15[a]	1059 ± 19	858 ± 20[a]
Secchi depth (m)	0.19 ± 0.01	0.39 ± 0.02	1.06 ± 0.04
Temperature – surface (°C)	22.8 ± 0.4	21.2 ± 0.8	16.3 ± 0.4
Temperature – bottom (°C)	22.4 ± 0.4	21.06 ± 0.7	16.3 ± 0.4
Dissolved oxygen – surface (mg L^{-1})	10.1 ± 0.6[a]	9.0 ± 0.3[a]	7.7 ± 0.3
Dissolved oxygen – bottom (mg L^{-1})	1.9 ± 0.5[a]	0.9 ± 0.2[a]	1.2 ± 0.3[a]
pH	9.9 ± 0.1	8.95 ± 0.04	8.05 ± 0.08
Alkalinity (mg $CaCO_3$ L^{-1})	66 ± 3	98 ± 5	140 ± 2
Chlorophyll *a* (μg L^{-1})	466 ± 30	200 ± 18	47 ± 3
Total P (μg L^{-1})	689 ± 198	278 ± 107	71 ± 40
SRP (μg L^{-1})	345 ± 13	54 ± 11	16 ± 2
Total N (μg L^{-1})	2300 ± 119[a]	1887 ± 102[ab]	1876 ± 201[b]
Ammonia (μg L^{-1})	57 ± 8[a]	64 ± 8[a]	1304 ± 180
Rotifers (no. m^{-3})	0[a]	0[a]	4 ± 4[a]
Daphnia carinata (no. m^{-3})	3 ± 2	2 ± 1	2933 ± 537
Chydoridae (no. m^{-3})	0[a]	0[a]	0.2 ± 0.1[a]
Mesocyclops sp. (no. m^{-3})	20041 ± 2866[a]	11287 ± 1493[a]	5992 ± 1812
Microcyclops sp. (no. m^{-3})	162 ± 56[a]	134 ± 25[a]	40 ± 17
Calamoecia sp. (no. m^{-3})	0.03 ± 0.03[a]	0[a]	11.8 ± 5.4
Anisops sp. (no. m^{-3})	8 ± 2[a]	5 ± 1[a]	0.1 ± 0.1
Agraptocorixa hirtifrons (no. m^{-3})	4 ± 1	0.6 ± 0.3[a]	0.1 ± 0.1[a]
Micronecta robusta (no. m^{-3})	2 ± 1	0.1 ± 0.1[a]	0.2 ± 0.1[a]

except for minima of 376 μg L^{-1} and 1327 μg L^{-1} recorded on 8 November 1988 and 24 October 1989 respectively. Ammonia and TKN were both poorly correlated with other parameters. Ammonia showed strong seasonal trends, being low in summer and high in winter–spring (57 ± 8 and 1304 ± 180 μg L^{-1} respectively).

Algae

Sixteen genera of algae were recorded: 9 Chlorophyta, 2 Cyanobacteria and 5 Chrysophyta (Fig. 4). *Microcystis aeruginosa, Pediastrum, Tribonema* and *Microspora* were collected throughout most or all of the year. *Oedogonium*, *Chlamydomonas*, *Anacystis*, *Ulothrix*, *Fragilaria* and diatoms were found only in spring, whereas *Scenedesmus* and *Ankistodesmus* were recorded only during late summer and autumn. Two benthic genera, *Cladophora* and *Spirogyra,* were collected on only one occasion.

Blooms of *M. aeruginosa* occurred throughout summer and autumn, peaking on 13 December 1988 with a chlorophyll *a* concentration of 705 μg L^{-1} and a Secchi depth of 0.13 m. Secchi depth extended to the lake bed in winter–spring, despite chlorophyll *a* concentrations reaching 83 μg L^{-1}. The shallow water depth truncated the Secchi depth readings during winter. There were strong relationships between algal utilization of CO_2 for photosynthesis and changes in pH and alkalinity. Total alkalinity was high (48–157 mg $CaCO_3$ L^{-1}) presumably because of limestone in the catchment. The pH was >10 between 13 December 1988 and 8 January 1989, CO_3^{-2} became the dominant form of carbon, and on the latter date no bicarbonate was recorded. High concentrations of free CO_2 and HCO_3^{-2} and pH <8.7 were recorded in winter. Throughout summer the water was frequently supersaturated with oxygen (up to 160% saturation or 14 mg L^{-1}), but in winter oxygen levels dropped to <6 mg L^{-1} and a mass kill of carp (*Carassius auratus*) was recorded at this time. Low concentrations of oxygen (<3 mg L^{-1}) were recorded at the bed of the lake throughout the year; these measurements probably represent the sediment oxygen levels rather than an anoxic layer of water, because the softness of the sediment prevented accurate discrimination of the sediment–water interface.

Zooplankton

Nineteen taxa were recorded in the plankton tows, but <10 taxa were recorded at any one time (Fig. 5). Two species dominated the zooplankton: *Daphnia carinata* (Cladocera) in winter accounted for >78% of the total abundance, and *Mesocyclops* sp. (Copepoda : Cyclopoida) in summer and autumn accounted for >95% of the total abundance. In late May 1989, the dominance changed between the two species.

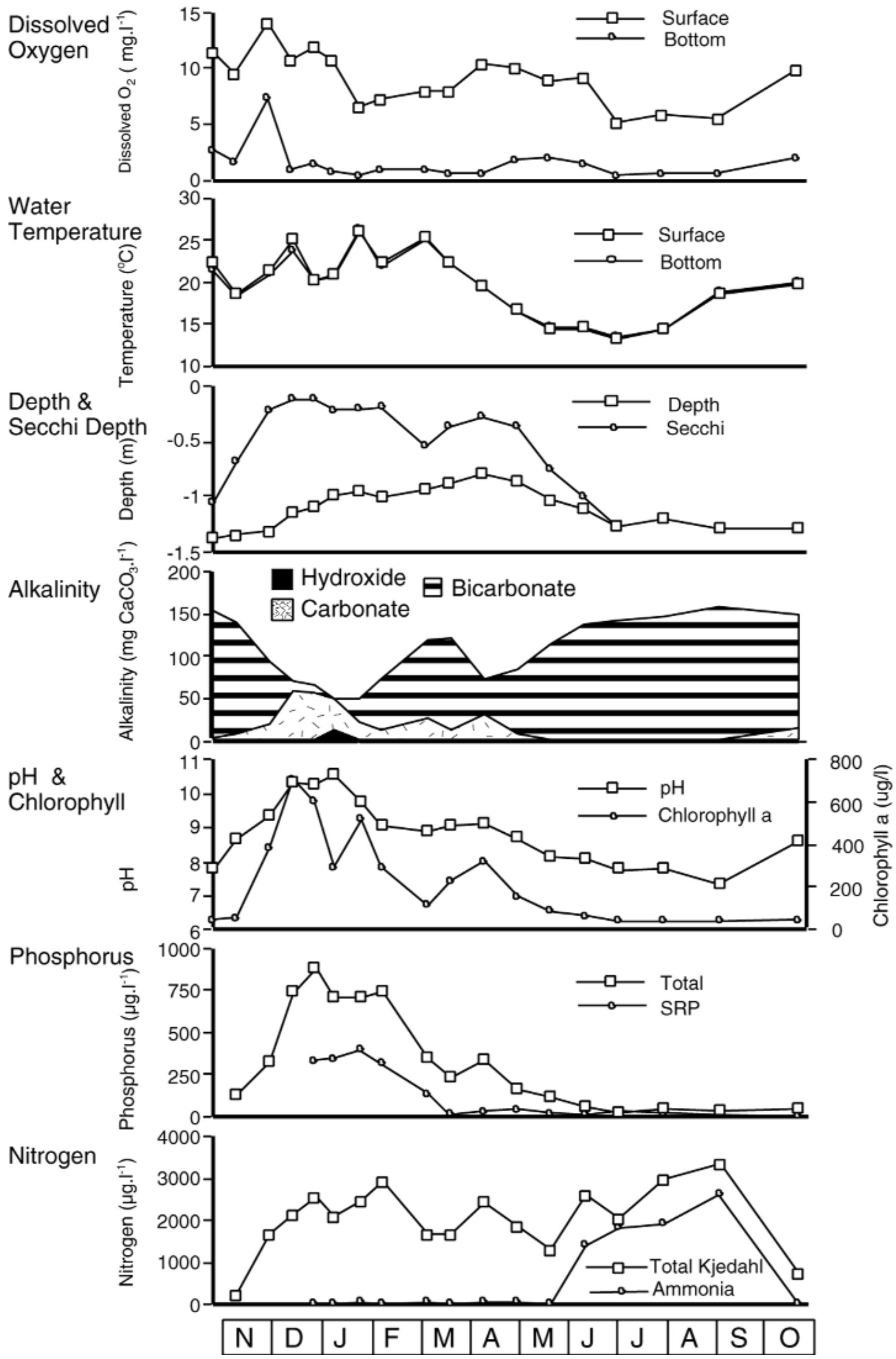

Fig. 3. Selected physico-chemical measurements for each sample period (means; s.e. not shown for clarity).

Preliminary data collected in September 1988 revealed high levels of *D. carinata* (12782 ± 4043 animals m^{-3}) and low levels of *Mesocyclops* sp. (322 ± 297 animals m^{-3}). These levels were very similar to those found in October 1989 and suggested that the spring changeover was likely to have occurred in October 1988 and November 1989.

The seasonal distribution of *D. carinata* and timing of egg production was similar to that recorded by Mitchell and Williams (1982*b*). In June, the maximum production of eggs, both parthenogenetic and ephippial, was recorded in the lake, followed by an increase in the population size and a 50% reduction in chlorophyll *a* in July. A high proportion of

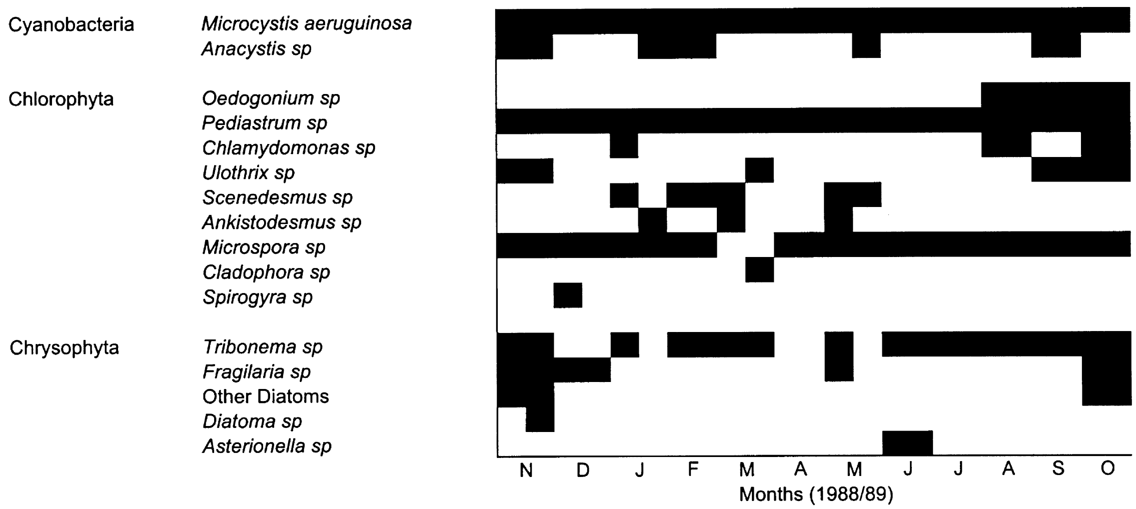

Fig. 4. Presence of algal genera (black shading) for each sample period.

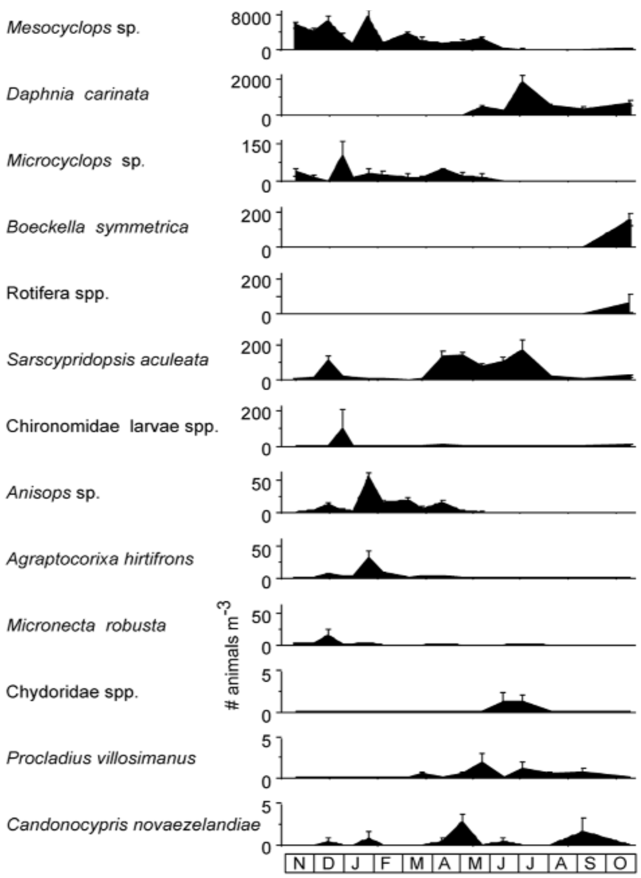

Fig. 5. Abundance (mean ± s.e.) of zooplankton species with more than a single occurrence.

D. carinata carried parthenogenetic eggs in summer (although this may have been an artefact of the small sample size) suggesting that the species was capable of surviving and breeding throughout summer and autumn.

Gravid *Mesocyclops* sp. specimens were common in November and early December, but also occurred throughout the remainder of summer and autumn. Very little breeding appeared to take place during winter. Other planktonic species were generally present in low numbers, the exception being *Microcyclops* sp. (Copepoda : Cyclopoida), which was abundant in summer but not recorded in winter. Rotifers were recorded in the phytoplankton samples in summer and autumn, but not in October when they were found in low numbers in the zooplankton samples. *Boeckella symmetrica* (Copepoda : Calanoida) and the predominantly benthic Chydoridae (Cladocera) (Robertson 1988) were recorded from August to October and June to July respectively. Chydoridae and rotifers were probably undersampled by the methods employed in this study.

Chironomid larvae (first and second instars only) were collected in plankton samples as they enter the plankton for passive dispersal (Davies 1976). Pupae were occasionally recorded, despite most local species emerging at night (Edward 1964). Chironomidae were mainly collected in summer, when large numbers are present in the benthos of the lake (Pinder *et al.* 1991). Several non-planktonic species were caught while feeding or replenishing air (e.g. Hemiptera (*Anisops* sp., *Agraptocorixa hirtifrons* and *Micronecta robusta*), larval coleopterans, zygopterans, dipterans and oribatid mites), or because the shallow depth meant that benthic and open-water habitats tended to overlap (e.g. ostracods).

The strong seasonal shift in dominance from *Mesocyclops* sp. to *D. carinata* between summer and winter was reflected in large positive or negative correlations, respectively, between the abundance of these species and Secchi depth, chlorophyll *a*, TP and alkalinity. Similar correlations were not recorded between any other species of zooplankton and water quality parameters. Vectors significantly correlated ($r > 0.7$, $P < 0.05$) with the zooplankton and phytoplankton

Table 2. Simple linear regressions between trophic levels (as in McQueen *et al*. 1986) in Lake Monger 1988–89
($lg = \log_{10}(x+1)$)

Chlorophyll *a* and nutrients (Bottom-up control)	
lg Chlorophyll *a* = 0.157 + 0.864 lg Total P	$r^2 = 0.846$
lg Chlorophyll *a* = 1.377 + 0.437 lg SRP	$r^2 = 0.452$
lg Chlorophyll *a* = 0.977 + 0.359 lg Total N	$r^2 = 0.052$
lg Chlorophyll *a* = 2.968 – 0.414 lg Ammonia	$r^2 = 0.505$
Chlorophyll *a* and zooplankton grazers (Top-down control)	
lg Chlorophyll *a* = 2.497 – .0.252 lg *Daphnia carinata*	$r^2 = 0.701$
lg Chlorophyll *a* = 1.11 + 0.297 lg *Mesocyclops* sp.	$r^2 = 0.539$
lg Chlorophyll *a* = 1.964 + 0.168 lg *Microcyclops* sp.	$r^2 = 0.164$
lg Chlorophyll *a* = 2.178 – 0.345 lg *Boekella symmetrica*	$r^2 = 0.112$
Zooplankton grazers and invertebrate predators (Top-down control)	
lg *Daphnia carinata*= 1.794 – 1.789 lg *Agraptocorixa hirtifrons*	$r^2 = 0.158$
lg *Daphnia carinata*= 2.386 – 2.222 lg *Anisops* sp.	$r^2 = 0.452$
lg *Mesocyclops* sp. = 2.874 + 1.349 lg *Anisops* sp.	$r^2 = 0.301$
lg *Microcyclops* sp. = 0.649 + 0.8 lg *Anisops* sp.	$r^2 = 0.11$
lg *Boekella symmetrica* = 0.235 – 0.227 lg *Anisops* sp.	$r^2 = 0.056$

ordination spaces are shown in Figs 2*b* and 2*c*. Depth, Secchi depth, ammonia (zooplankton only) and to a lesser extent alkalinity were associated with the winter group in both plots. Only temperature was correlated with the summer group in zooplankton. pH, SRP, TP, and chlorophyll *a* were associated with the separation between the winter and summer–autumn groups rather than with either summer or autumn directly.

McQueen *et al*. (1986) examined the strength of the relationships between trophic levels in pelagic freshwater systems using simple linear regressions between trophic components. In Lake Monger (Table 2), both TP and *D. carinata* were strongly related with chlorophyll *a*. The r^2 value for the *D. carinata*–chlorophyll *a* relationship was very similar to that recorded by McQueen *et al*. (1986). SRP and ammonia accounted for 45% and 50% respectively of the variation in chlorophyll *a*. *Anisops* sp. may be a significant predator of *D. carinata*, because it accounted for 45% of the variability in *D. carinata* abundance.

Discussion

Lake Monger was hypertrophic, as defined by Wetzel (1983) (summer maxima >100 μg L^{-1} P) over 1988–89. This classification is based on temperate lakes but, as suggested by Davis *et al*. (1993) and Lund (in press), the warm-water (minimum water temperature >10°C) scheme of Salas and Martino (1991) may be more appropriate for SCP wetlands. Considering the latter classification scheme and each seasonal grouping separately, Lake Monger is hypertrophic in summer, eutrophic in autumn, and approaching mesotrophic in winter–spring. These results indicate that it may be uninformative to assign a single trophic classification to the highly seasonal wetlands of the SCP.

Top-down relationships

Although Mitchell (1986) found generally complex calanoid copepod communities in Australian lakes, only one species of calanoid was recorded at Lake Monger. Waterbodies in New South Wales of a similar size to Lake Monger typically contain *Mesocyclops leuckarti* [sic; this species is now known not to occur in Western Australia, although the genus does (R. Shiel, personal communication)], *Boeckella* sp., sometimes *Calamoecia* sp. and one or two cladocerans (Timms 1970). Similarly, Lake Monger contained two cyclopoids (*Mesocyclops* and *Microcyclops*), one calanoid (*B. symmetrica*) and two cladocerans (*D. carinata* and Chydoridae).

The timing of the appearance of *B. symmetrica* between August and October was similar to that recorded for *Boeckella triarticulata* by Mitchell and Williams (1982*a*). Their appearance coincides with the changeover in dominance between *D. carinata* and *Mesocyclops* sp., suggesting that this may be a brief period when conditions are favourable for *B. symmetrica*. The rapid increase in the abundance of the predatory fish *Gambusia holbrooki* (Girard) (Lund 1992) at the end of October could have caused this to end (Maly and Maly 1997). *Microcyclops* sp., a herbivorous copepod, was absent in winter, possibly because of the temperature, food requirements or possibly competitive exclusion by *D. carinata*. Koste *et al*. (1983) found that the distribution and density of the rotifer fauna was very variable in Western Australian wetlands. In the present study, rotifers were found in Lake Monger throughout most of late spring to early autumn, when *Mesocyclops* sp. was dominant, despite the suggestion of Koste *et al.* (1983) that cyclopoid copepods were capable of limiting rotifer populations. Competition for food resources (Kerfoot 1977; Hurlbert and Mulla 1981) or mechanical interference (Wickham and Gilbert 1991) by large cladocerans may explain the absence of rotifers from the lake in winter. Although seasonal effects appear to be important, the interactions among zooplankton species also need to be examined experimentally (see Maly and Maly 1997).

There were strong relationships between TP and *D. carinata* and between TP and chlorophyll *a*, indicating the potential importance of both top-down and bottom-up controls of algal biomass within the lake. Water quality in the lake in December 1990 and January 1991 improved substantially, with Secchi depths extending to the bed, chlorophyll *a* <80 μg L^{-1} and TP <150 μg L^{-1} (Lund 1992). Changes were also seen in the zooplankton fauna with *Calamoecia tasmanica subattenuata* (Copepoda : Calanoida) and *D. carinata* being dominant, low numbers of *Mesocyclops* sp. and rotifers and the absence of *Microcyclops* sp. (Lund 1992).

The success of a biomanipulation is contingent on maintaining large populations of large-bodied cladocerans (e.g. *D. carinata*) in the lake throughout the summer. Summer declines in *Daphnia* populations have been ascribed to water renewal, temperature, invertebrate predators, vertebrate predators and food resources (Threlkeld 1987), although Wright and Shapiro (1990) suggest that loss of refugia rather than reductions in natality are important. Refugia are created by gradients of temperature, light and oxygen, which generally occur at depths >2 m. Such depths do not occur in Lake Monger. The lake receives comparatively few inputs of water during summer, and so water renewal is also unlikely to be responsible for the summer decline in *D. carinata.* Mitchell and Williams (1982*a*) and Hebert (1977) believed *D. carinata* to be a cold-water species, because it was not recorded during summer. However, Davis *et al*. (1993), Lund (1992) and the present study all recorded the presence of *D. carinata* in Perth wetlands during summer, sometimes in high numbers.

The observed alternation in dominance between *Mesocyclops* sp. and *D. carinata* is unlikely to be a direct interaction. *Mesocyclops* sp. is carnivorous (Fryer 1957), but Kerfoot (1977) found the preferred size range of prey to be substantially smaller than *D. carinata*. Notonectids (*Anisops*) are important predators of *D. carinata* and are capable of regulating populations in ponds (Benzie 1991; Geddes 1986); *Anisops* accounted for 45% of the variation in *D. carinata* in the lake. Predation by *Anisops* does not appear to be very important, because development of a defensive crest was not observed in *D. carinata,* and *Anisops* abundance peaked two months after the decline in *D. carinata*. Corixids (*A. hirtifrons*, *M. robusta*), which can eat small invertebrates, do not appear to influence *D. carinata* populations (r^2 <0.15). *Gambusia holbrooki* was the most abundant fish in the lake during summer, and it does eat *D. carinata* (gut contents analysis, Lund unpublished). *Gambusia* can substantially alter zooplankton community structure by reducing the abundance of large-bodied cladocerans (Hurlbert and Mulla 1981; Lancaster and Drenner 1990). The occurrence of high densities of both *D. carinata* and *G. holbrooki* in summer 1990–91 suggests that fish predation may not be of great importance.

The most probable cause for the observed summer decline in *D. carinata* was changes in the food resources. Mills *et al*. (1987) found that *Daphnia* produced ephippial eggs at the end of a clear-water phase, in response to food limitation. Ephippial eggs were produced in reasonable numbers in June and September, indicating possible food limitation at these times. *Microcystis aeruginosa* (Cyanobacteria) became increasingly dominant in the lake in September. Mitchell and Williams (1982*b*) considered *D. carinata* to be a facultative browser, but the ability of *Daphnia* to use Cyanobacteria is contentious (see review in Burns 1987). Matveev *et al*. (1994) found that *D. carinata* showed no adverse effects from grazing on small colonies of *Microcystis* (see also Carlson and Schoenberg 1983; Merrick and Ganf 1988). *M. aeruginosa* may have been present in colonies too large to be edible or too nutritionally poor to sustain *Daphnia* populations during summer (see review in Boon *et al*. 1994). *Microcystis aeruginosa* was present in the phytoplankton in summer 1990–91, but no blooms were recorded. Concentrations of TP <150 μg L^{-1} in summer appear to allow large populations of *D. carinata* to develop. These results suggest that a reduction in nutrient levels in the lake to reduce the dominance of *M. aeruginosa* is needed for a biomanipulation of the lake to succeed.

Bottom-up relationships

The low TP : TKN (<12) ratio recorded at Lake Monger between spring and autumn, and the high levels of SRP, indicate likely N limitation. Nitrogen limitation in summer has also been recorded in North Lake (Perth) by McDougall and Ho (1991). The low concentrations of ammonia (this study) and nitrate/nitrite (January 1989; Davis *et al*. 1993) found in summer also indicate N limitation. However, TP accounted for 85% of the variation in chlorophyll *a*. Comparison of the slope (0.86) of the regression with those of Lund (in press) and Ferris and Tyler (1985) revealed that it was within the range (0.84 to 1.58) encompassed by other Australian and overseas studies. The low value of the slope suggests possible N limitation. Cargeeg *et al.* (1987) found that groundwater near Lake Monger contained nitrate levels of ~1 mg L^{-1}; these levels appear to decline rapidly in the sediment, where Davis *et al.* (1991) recorded nitrate levels of <20 μg L^{-1} in interstitial waters. TKN recorded for lake sediments in 1989 was 8.6–12.3 mg g^{-1}, which was low compared with the other SCP wetlands (Davis *et al.* 1993). The apparent loss of nitrates in the sediments suggests that denitrification may be a significant process within the lake, contributing to the N limitation for algae in summer. The dominance of *M. aeruginosa* throughout the summer suggests that N did not remain limiting for long periods, otherwise a N-fixing cyanobacterium would probably have become dominant. Carbon may limit algal growth during intense blooms, because on one occasion no bicarbonate was recorded. This limitation was likely to be only temporary because CO_2 readily diffuses into the water column (Moss 1988). The low carbon dioxide concentrations that occurred during summer may be responsible for the domination of Cyanobacteria over other algal taxa (see review by Shapiro 1990). Davis *et al*. (1993) found that the ratio of mean maximum depth to depth of euphotic zone (Z_m/Z_e) for the lake was 0.35, indicating that light should not be limiting; however, with Secchi depths of <0.25 m recorded in summer, self-shading could have been important (McDougall and Ho 1991).

As the lake appears to be N limited, the addition in spring–summer of fertilizers containing N that can be captured by groundwater may be important in triggering algal blooms. Perth City Council ceased fertilizing the lawns in January 1990, and this appears responsible for the substantial improvements seen in water quality in summer 1990–91 and subsequent years. Fertilizer applications on lawns at Lake Claremont increased TP levels in groundwater from 0 to 200 $\mu g\ L^{-1}$ and SRP levels from 14 to 45 $\mu g\ L^{-1}$ (Lantzke *et al.* 1989). The first winter rains increased groundwater concentrations of inorganic N from 1500 to >2500 $\mu g\ L^{-1}$ from fertilizer applications around Blue Gum Lake (SCP) (Carbon *et al*. 1988). Intensive irrigation of the lawns at Lake Monger appears to be rapidly transporting nutrients into the lake during summer. Davis *et al* (1993) found nitrate+nitrite concentrations in the lake water of 12 $\mu g\ L^{-1}$ in January 1989 and of 85 $\mu g\ L^{-1}$ in September 1989, rising to >300 $\mu g\ L^{-1}$ in November 1989. Between 1985 and 1987, nitrate+nitrite concentrations were always higher in the lake following fertilizer applications (Davis and Rolls 1987). Davis *et al.* (1991) recorded ammonia concentrations in summer 1991 of >2500 $\mu g\ L^{-1}$ in the interstitial waters of Lake Monger, probably due to ammonification of organic matter in the sediments. Lund *et al*. (1991) and Qiu and McComb (1994) recorded >30% loss on ignition of Lake Monger sediments. Anoxia in the sediments allows ammonia to accumulate and create a diffusion gradient, which results in release to the water column (Wetzel 1983). The differences between winter and summer ammonia concentrations recorded in the present study are probably due to rapid utilization of any available ammonia by algae in summer. Davis and Rolls (1987) recorded similar winter peaks of ammonia in two other similar SCP wetlands in 1985 and 1986.

Internal P release from sediments in shallow lakes over summer (e.g. Jacoby *et al*. 1982; Marsden 1989) can be a serious impediment to lake rehabilitation. The P in the Lake Monger sediments was bound in the approximate fractions 42% apatite-P, 25% non-apatite-P and 33% organic-P (Davis *et al*. 1993). The high proportion of apatite-P is a reflection of the limestone aquifer. Lake Monger has relatively high Fe and Mn components in the sediment (241–324 and 280–460 $mg\ g^{-1}$ dry wt respectively), which are the highest and an order of magnitude greater than in most of the other wetlands sampled by Davis *et al.* (1993) on the SCP. Phosphorus bound to Fe and Mn is the most likely source for internal release, because the high pH of the water in summer would substantially reduce apatite-P solubility (Golterman 1984). The highly mixed nature of the water column is likely to keep the sediment surface oxidized. Water temperature in the lake (summer minimum 19°C) correlated strongly with TP and SRP. At temperatures above 17–21°C, P release from the sediments can become independent of oxygen concentrations in the water column (Marsden 1989) because bacterial oxygen demand can break down the aerobic microzone, allowing anaerobic release of P (as in Mortimer 1941). Bioturbation of sediments by chironomid larvae and tubificids can result in P release independent of oxygen concentrations (Holdren and Armstrong 1980; Pinder *et al*. 1991). Pinder *et al*. (1991) and Edward (1964) have recorded high abundances of these organisms during summer (>3000 chironomids m^{-2}) in the lake, which may make a significant contribution to P release. Moss *et al.* (1986) believed the rain of labile organic matter from summer algal blooms was responsible for the breakdown of the oxidized microzone of the sediment, allowing P release. As mean air temperature in 1990–91 (November–January) was higher than in 1988–89 (24.77 ± 0.67°C and 22.95 ± 1.28°C respectively), this mechanism may be more important than bacterial oxygen demand. It appears likely that the fertilizer application to the lake in September–October 1988 was sufficient to trigger an algal bloom that was sustained by internal release until autumn 1989. The absence of a fertilizer application in spring 1990 prevented an initial bloom, which appears sufficient to prevent the build-up of the organic matter required to stimulate internal release. Moss *et al*. (1986) found that water quality improved substantially and macrophytes returned to two lowland lakes two years after isolation. The build-up of organic matter from the submerged macrophytes eventually resulted in the reversion of the system back to phytoplankton dominance. The regular growth of submerged macrophytes in Lake Monger since 1991–92 may indicate a possible return to a phytoplankton-dominated system in the future.

Implications for biomanipulation

Nutrient concentrations in the lake were substantially lower in 1990–91 because of a change in catchment management, but they were still high in comparison with undisturbed wetlands. The low algal biomass recorded at this time may have been due to the grazing pressure exerted by high numbers of *D. carinata*. Water temperature did not appear responsible for the decline in *D. carinata* within the lake in 1988–89, given the higher temperatures of 1990–91. The abundance of *D. carinata* in 1990–91 indicated that *G. holbrooki* or invertebrate predators were unable to limit the populations. This suggests that inedible or nutritionally poor algae may have been responsible for the decline in *D. carinata* in the summer of 1988–89. *Mesocyclops* sp. densities in 1990–91 were similar to those recorded in winter 1989, which suggests that there is a competitive relationship between *Mesocyclops* sp. and *D. carinata*. This is unlikely to be direct but may be mediated through another species; a possible candidate is *Microcyclops* sp. which was not recorded in 1990–91 but was abundant in summer 1988–89. *Microcyclops* is believed to be a grazer and may be competitively excluded by high abundances of *D. carinata. Microcyclops* sp. appears to be an important food source for *Mesocyclops* sp.

The results of this study indicate that top-down control in Perth lakes by *D. carinata* may not be limited by predation or temperature but by the presence of inedible or nutritionally poor algae. As a consequence, it may not be possible to increase the abundance of large-bodied cladocerans without reducing nutrient concentrations. This finding emphasizes the importance of catchment management to reduce nutrient inputs, in addition to in-lake control of nutrients (possibly through sediment remediation) as part of a suite of approaches, including biomanipulation, for restoration of eutrophic wetlands in south-western Australia.

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